

Hatching Depth of *Nautilus pompilius* in Fiji

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Abstract. Analyses of oxygen and carbon isotopes in the shell and septa of *Nautilus* have shed light on the early life history of this animal. Previous studies have shown that $\delta^{18}\text{O}$ is a reliable indicator of the temperature and, by inference, the depth at which the shell material forms. Thus, it is clear that *Nautilus* hatches at 22–24°C, corresponding to a depth of 100–200 m, depending on the location; thereafter, animals migrate to colder, deeper water (300–400 m depth). However, Davis & Mohorter (1973) reported the capture of three specimens of newly hatched *Nautilus* in shallow water (1.25 m deep) in Korolevu Bay, Viti Levu, Fiji. To resolve this paradox, we analyzed the isotopic composition of the septa and apertural margin in two of these specimens. The specimens are approximately 25 mm in diameter and show the nepionic constriction on the outer shell and a reduction in septal spacing, features that indicate the point of hatching. The oxygen isotope values of the embryonic septa in both specimens range from -0.77 to -0.55‰ , corresponding to an average temperature of 22.6°C and a depth of 160 m (based on temperature-depth profiles in the area). The values of $\delta^{18}\text{O}$ of the postembryonic septum and apertural margin are 1.33 and 0.99‰, respectively, in one specimen (corresponding to 14°C, 370 m depth), and 0.42 and 0.53‰, respectively, in the other specimen (corresponding to 17°C, 300 m depth). The values of $\delta^{13}\text{C}$ also show a marked difference between embryonic and postembryonic shell material (-0.82 to 0.67‰ in embryonic and -2.40 to -1.06‰ in postembryonic shell material). Thus, these animals did not hatch in shallow water, but exhibited the same pattern as that of other *Nautilus* from Fiji: hatching at a depth of 160–210 m, followed by a descent to a depth of 300–370 m. Thereafter, these animals apparently migrated or were transported (by currents?) to shallow water where they were captured; the geographic distance involved was 1.5 km (based on bathymetric charts). Reports of drifted shells of approximately the same size collected in the same area and elsewhere indicate that this post-hatching behavior may not be uncommon and may well be fatal.

INTRODUCTION

Davis & Mohorter (1973) reported the capture of three small juveniles of *Nautilus* in Korolevu Bay on the southwest coast of Viti Levu, Fiji (Figure 1). The specimens are approximately 25 mm in diameter and, on the basis of their morphological features, appear to have been newly hatched (Figure 2). What is astonishing is the shallow depth at which these animals were collected—only 1.25 m. That report constitutes the only published account of newly hatched *Nautilus* in the wild.

The implication of this finding was that the animals had hatched in shallow water. Nevertheless, this occurrence was considered anomalous. Chamberlain (1978) doubted that juvenile *Nautilus* could survive the turbulence in such shallow water. Ward & Martin (1980) argued that the temperatures near the surface would be lethal to young animals. In addition, they reasoned, if breeding and hatching occur in shallow water, why had they and others failed to find more animals at those depths during subsequent searches. Moreover, one of us (R. A. D.) visited Korolevu and interviewed local inhab-

itants, none of whom could recall seeing small individuals of *Nautilus*.

In the two decades after the Mohorter specimens were collected, studies of the carbon and oxygen isotope record of *Nautilus* shed new light on the question of hatching depth (Eichler & Ristedt, 1966a, b; Cochran et al., 1981; Taylor & Ward, 1983; Oba & Tanabe, 1983; Oba et al., 1992). These studies revealed a characteristic pattern of light $\delta^{18}\text{O}$ values for embryonic septa followed by a marked shift toward heavier values for postembryonic septa.

To help explain this pattern, Landman et al. (1994) analyzed the isotopic record in *Nautilus belauensis* Saunders, 1981, raised in aquaria under controlled temperature conditions. They concluded that both the embryonic and postembryonic septa of *Nautilus* are secreted with the same temperature-dependent fractionation of aragonite relative to water as that of other aragonite-secreting mollusks (Grossman & Ku, 1986). The $\delta^{18}\text{O}$ values of the septa thus provide a reliable means of determining the water temperature, and, by inference, the depth at which the septa form.

Using the results of this study, Landman et al. (1994)

interpreted the oxygen isotope patterns of specimens caught in the wild. These analyses indicated that hatching occurs at 22–24°C, corresponding to a depth of 100–200 m, depending on the location. In particular, in Fiji, it occurs at an average temperature of 22°C, corresponding to a depth of about 190 m. The abrupt increase in $\delta^{18}\text{O}$ observed in postembryonic septa reflects migration to colder, deeper water after hatching.

In light of these data, we investigated the record of carbon and oxygen isotopes in the specimens described by Davis & Mohorter (1973). The specimens are repositied in the Cincinnati Museum of Natural History (CMNH), and permission was obtained to sample them for isotopic analyses.

BACKGROUND

Davis & Mohorter (1973) described three specimens of *Nautilus* from Fiji (CMNH 74-103 A–C), which they referred to as *Nautilus* cf. *N. pompilius* Linnaeus, 1758. In the intervening years, many studies have demonstrated that the only species of *Nautilus* present in Fiji is *N. pompilius* (see Ward & Martin, 1980; Ward, 1987; House, 1987; Hayasaka et al., 1987; Saunders, 1987; Saunders & Ward, 1987; Tanabe et al., 1990). We therefore regard these specimens as *N. pompilius*, although it is difficult to differentiate juvenile shells of the various species of *Nautilus* purely on the basis of morphology or color.

Of the three specimens, two were caught between February 22 and the end of March, 1955 in the lagoon behind the barrier reef in Korolevu Bay, Viti Levu (Figure 1, A on map). They were found in a hole in a submerged rock at a depth of about 1.25 m. The third specimen was caught between January 1 and February 2, 1958, also in a hole in a submerged rock in Korolevu Bay (Figure 1, B on map). Unfortunately, which specimen was collected where was not recorded at the time the specimens were captured.

At the mouth of Korolevu Bay, there is a break in the barrier reef 0.3 km wide. On the seaward side of the reef, the water deepens rapidly, attaining a depth of 1000 m in a distance of 3 km (slope = 18°) (Holmes, 1982). Ward et al. (1977) and Hayasaka et al. (1987) described similar steep submarine slopes off Suva on the southeast coast of Viti Levu.

We analyzed specimens 74-103 B and C (Figures 2A–D; see Davis & Mohorter, 1973:table 1). Specimen 74-103B is 26.1 mm in diameter, with nine septa and a reduction in septal spacing (septal approximation) between septa 8 and 9. Specimen 74-103C is 23.2 mm in diameter, with eight septa and a reduction in septal spacing between septa 7 and 8. Both specimens show the nepionic constriction just adapical of the apertural margin.

The reduction in septal spacing coincides in time of formation with the growth discontinuity (nepionic constriction) at the aperture, and both features demarcate the

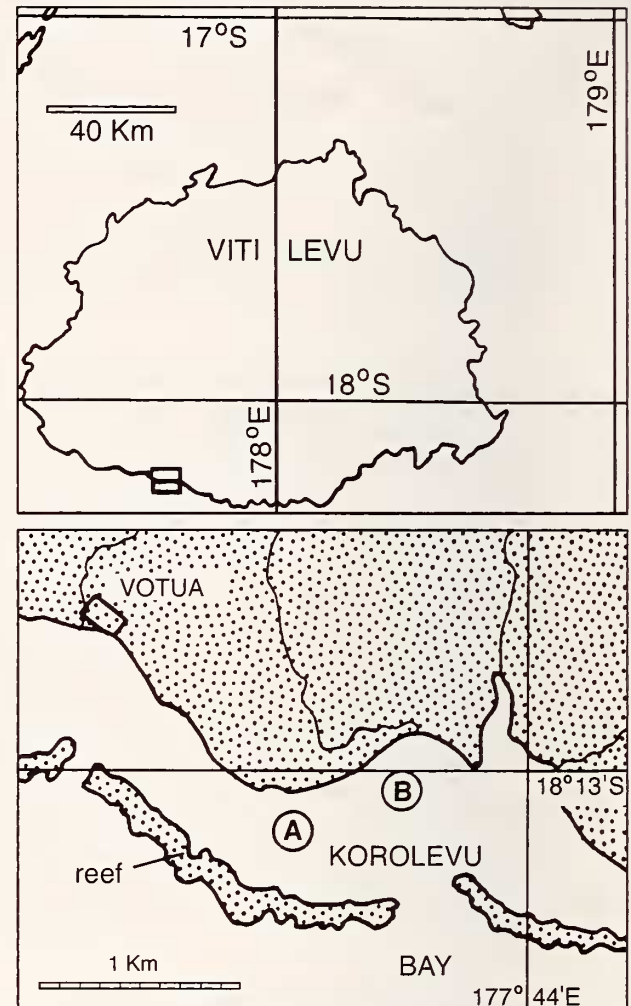


Figure 1. Index map (top) and close-up (bottom) of part of the Fiji Islands showing the localities (A, B) where the specimens of *Nautilus pompilius* Linnaeus, 1758, were captured. (Modified from Davis & Mohorter, 1973:fig. 1).

point of hatching on the shell (Arnold et al., 1987; Landman, 1988; Landman et al., 1994). Thus, specimen 74-103B hatched between septa 8 and 9, and septa 1–8 formed during embryonic development, and septum 9, during postembryonic development. Specimen 74-103C hatched between septa 7 and 8, and septa 1–7 formed during embryonic development, and septum 8, during postembryonic development. The outer shell grew slightly beyond the nepionic constriction in both specimens.

METHODS

Specimens were sectioned along the medial plane, and the septa were sampled for analysis. In addition, we sampled a small piece of shell at the apertural margin in each specimen. The samples, consisting of tiny pieces of aragonitic shell material, were crushed into coarse powders.

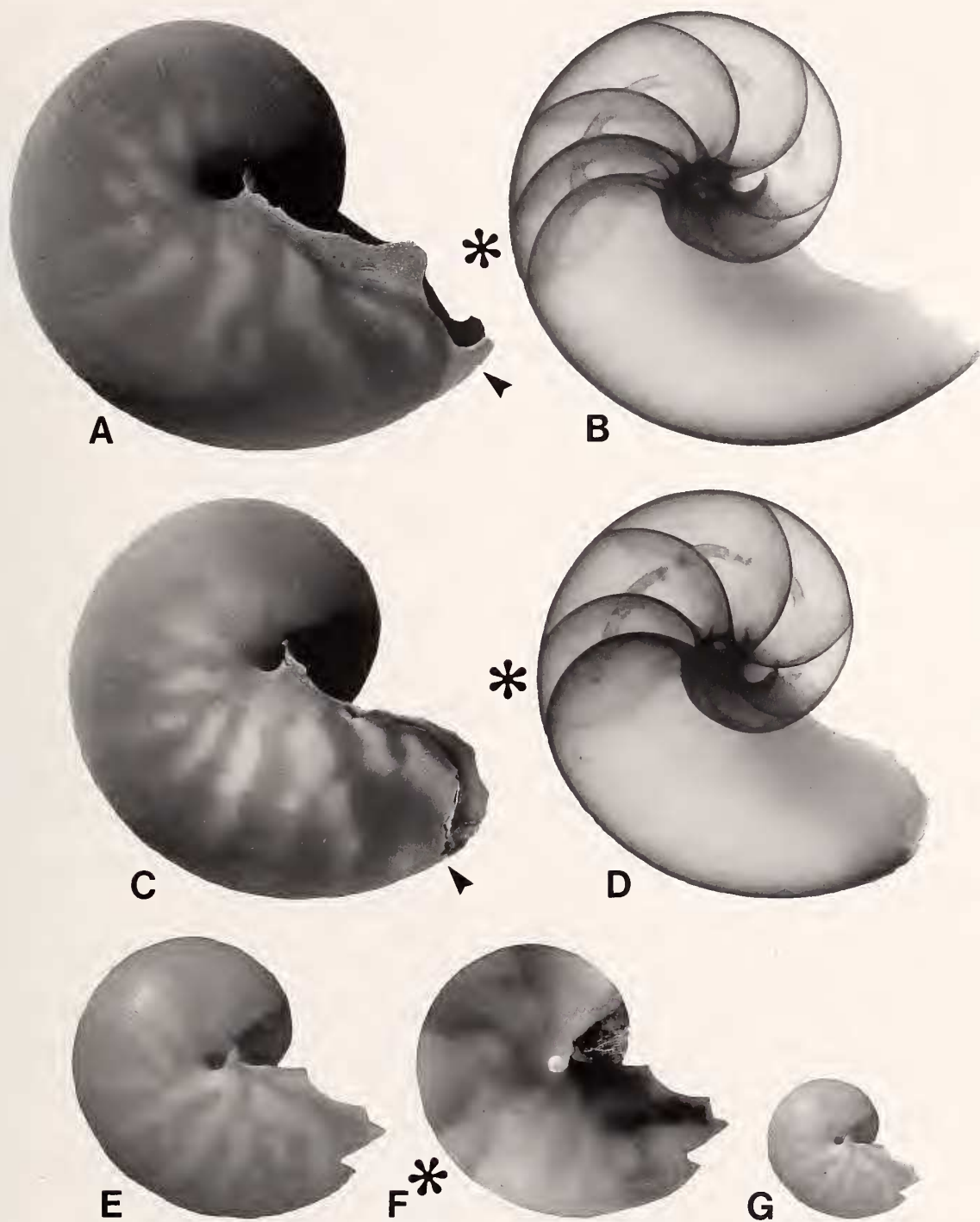


Figure 2. A, B. *Nautilus pompilius* Linnaeus, 1758, CMNH 74-103B, live-caught, Korolevu Bay, Fiji, diameter 26.1 mm. A. Right lateral view. B. Right lateral view, x-ray. C, D. *Nautilus pompilius*, CMNH 74-103C, live-caught, Korolevu Bay, Fiji, diameter 23.2 mm. C. Right lateral view. D. Right lateral view, x-ray. E-G. *Nautilus pompilius*, AMNH 44681, collected on the beach, Philippines, diameter 23.4 mm. E. Right lateral view. F. Right lateral view, transmitted light. G. Right lateral view. Arrows indicate the nepionic constriction; asterisks, septal approximation.

Table 1

Stable isotope data for the septa and apertural margin in two live-caught *Nautilus pompilius* Linnaeus, 1758, from Fiji. Temperatures of the water in which the shell material formed are based on the equation of Grossman & Ku (1986) for the temperature-dependent fractionation of aragonite in mollusks relative to seawater. Septa are numbered in their order of secretion.

Specimen	Septum	$\delta^{18}\text{O}$	$\delta^{13}\text{C}$	T(°C)
74-103B	1	-0.59	-0.08	22.30
74-103B	2	-0.64	-0.31	22.57
74-103B	3	-0.64	0.00	22.54
74-103B	4	-0.77	0.20	23.17
74-103B	5	-0.67	0.53	22.69
74-103B	6	-0.56	0.67	22.19
74-103B	7	-0.71	0.37	22.90
74-103B	8	-0.63	0.03	22.48
74-103B	9	1.33	-1.06	13.29
74-103B	aperture	0.99	-2.10	14.92
74-103C	1	-0.75	-0.82	23.05
74-103C	2	-0.67	-0.30	22.67
74-103C	3	-0.73	-0.15	22.99
74-103C	4	-0.61	-0.05	22.40
74-103C	5	-0.57	0.26	22.22
74-103C	6	-0.55	0.10	22.12
74-103C	7	-0.68	-0.14	22.75
74-103C	8	0.42	-1.29	17.58
74-103C	aperture	0.53	-2.40	17.08

The powders were cleaned using the hydrogen peroxide procedure outlined by Allmon et al. (1992) to remove organic contaminants. The cleaned samples were then analyzed according to standard techniques (McCrea, 1950) involving an initial reaction in vacuo with 100% orthophosphoric acid at 90°C for 0.25 hr. An on-line, automated carbonate preparation system facilitated the production and purification of the evolved CO₂ gas. The isotopic differences between the derived samples of CO₂ and the Peedee belemnite (PDB) standard were determined using the mass spectrometers in the Stable Isotope Laboratory in the Department of Geology at the University of Florida, Gainesville. Values of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ are reported relative to the PDB standard, and the precision ranges from 0.05‰ to 0.10‰.

RESULTS

The results of the isotopic analyses are listed in Table 1 and illustrated in Figure 3. The oxygen isotope values of the embryonic septa in the two specimens range from -0.77 to -0.55‰. In contrast, the values of $\delta^{18}\text{O}$ of the postembryonic septum and apertural margin are 1.33 and 0.99‰, respectively, in specimen 74-103B, and 0.42 and 0.53‰, respectively, in specimen 74-103C. The values of $\delta^{13}\text{C}$ also show a marked difference between embryonic and postembryonic shell material (-0.82 to 0.67‰ in

embryonic and -2.40 to -1.06‰ in postembryonic shell material).

DISCUSSION

According to Landman et al. (1994), both the embryonic and postembryonic septa of *Nautilus* are secreted with the same temperature-dependent fractionation of aragonite relative to water as that of other aragonite-secreting mollusks (Grossman & Ku, 1986). Therefore, it is possible to determine the temperature, and, by inference, the depth at which the shell material forms.

We used the equation derived by Grossman & Ku (1986) to determine temperature:

$$T(^{\circ}\text{C}) = 21.8 - 4.69(\delta_{\text{Ar}} - \delta_{\text{w}})$$

where T is the temperature in degrees Celsius, δ_{Ar} is the oxygen isotope composition of the aragonite, and δ_{w} is the oxygen isotope composition of the water as defined by Epstein & Mayeda (1953) and modified by Craig (1961). The value of δ_{w} in Fiji is presumed to be -0.28 (based on $\delta^{18}\text{O}$ [Standard Mean Ocean Water, SMOW] values of Oba et al. [1992] converted to δ_{w} according to the equation of Friedman & O'Neil [1977]).

The calculated temperatures for the two specimens are listed in Table 1 and plotted in Figure 4. The temperature of formation of the embryonic septa is remarkably uniform in both specimens, with an average of 22.6°C (SD = 0.33; n = 15). The calculated temperatures of formation of the postembryonic septum and apertural margin are 13.3°C and 14.9°C, respectively, in specimen 74-103B, and 17.6°C and 17.1°C, respectively, in specimen 74-103C.

We consulted temperature-depth profiles in the region of capture to determine the corresponding depths of shell formation. The best available data are those of Holmes (1982:fig. 3, probe 1) showing a profile off Somosomo Bay, 11 km east of Korolevu Bay, for August 11, 1982.

On the basis of these data, the embryonic septa in both specimens formed at a depth of 160 m. The temperatures of formation of the postembryonic septum and apertural margin correspond to a depth of 370 m (355–380 m) in specimen 74-103B and 300 m (300–310 m) in specimen 74-103C. These depth estimates are approximate because the temperature-depth profile we used does not match the actual time and site of capture, and because the calculated temperatures reflect averages over the time of formation of the shell material, implying that the corresponding depths also represent averages.

The pattern of $\delta^{13}\text{C}$ in the two specimens is also consistent with a change in depth. The values of $\delta^{13}\text{C}$ of the postembryonic septa and aperture in both specimens are markedly lighter than those of the embryonic septa (Table 1). This difference reflects the variation in $\delta^{13}\text{C}$ of the total dissolved inorganic carbon in the water column. The embryonic shell formed in shallow water that was de-

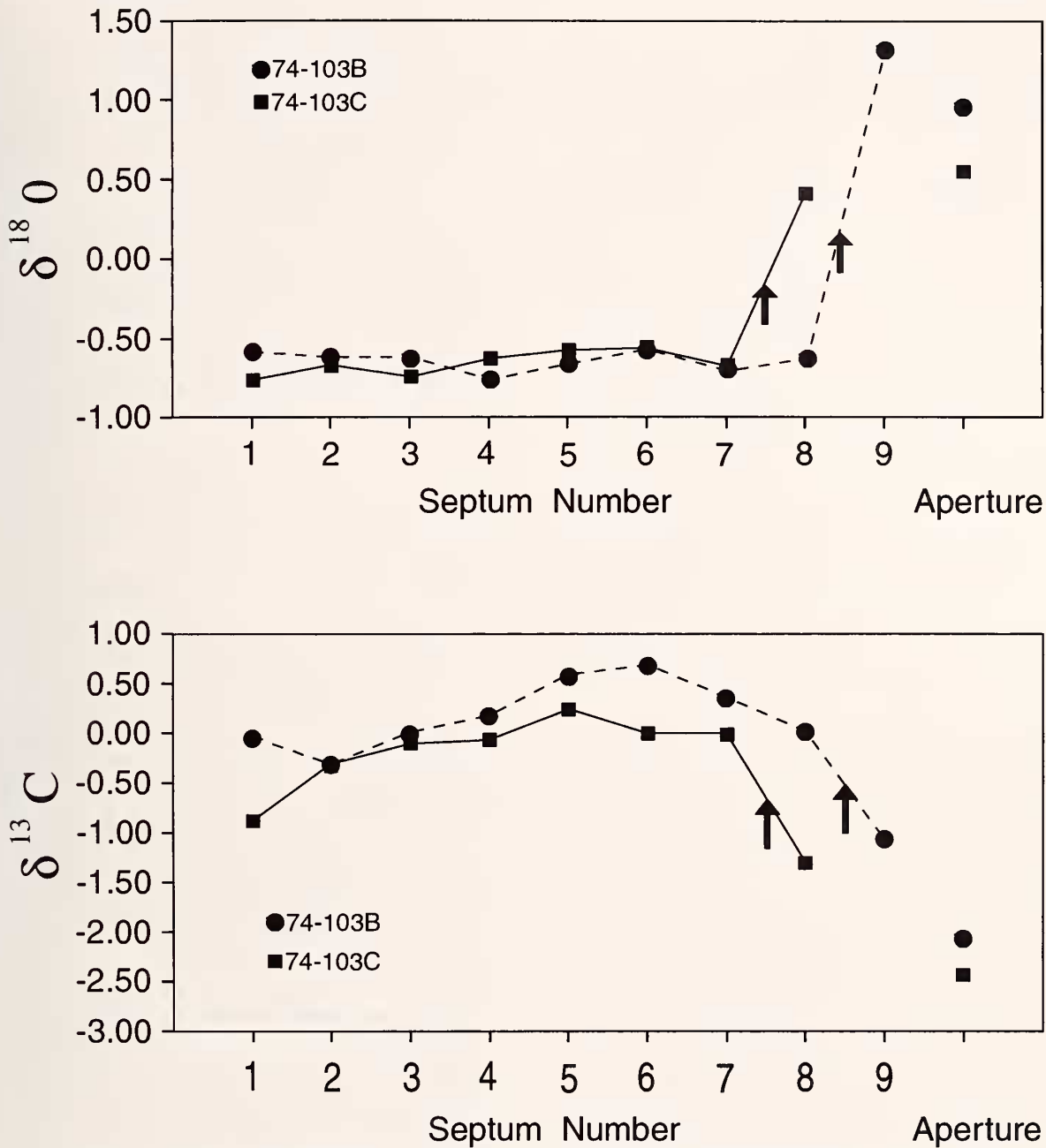


Figure 3. Values of $\delta^{18}O$ and $\delta^{13}C$ for samples of the septa and apertural margin in specimens 74-103B and 74-103C from Fiji. All values are relative to the PDB standard, and the precision ranges from 0.05‰ to 0.10‰. Septa are numbered in their order of secretion. The arrows indicate the point of hatching on each specimen.

pleted in ^{12}C by phytoplankton, whereas the postembryonic shell formed at greater depths where the $\delta^{13}C$ of the water (and hence the shell) was lighter due to regeneration of organic matter (Arthur et al., 1983).

Thus, these *Nautilus* did not hatch in the shallow lagoon in which they were collected. Instead, they must have followed the pattern inferred for other specimens

from Fiji: embryonic development and hatching at 21–23°C, corresponding to a depth of 160–210 m. After hatching, the animals descended to colder, deeper water (300–370 m deep).

There are several possible explanations for the presence of these animals in the lagoon. According to bathymetric charts (Holmes, 1982:fig. 2), the geographic dis-

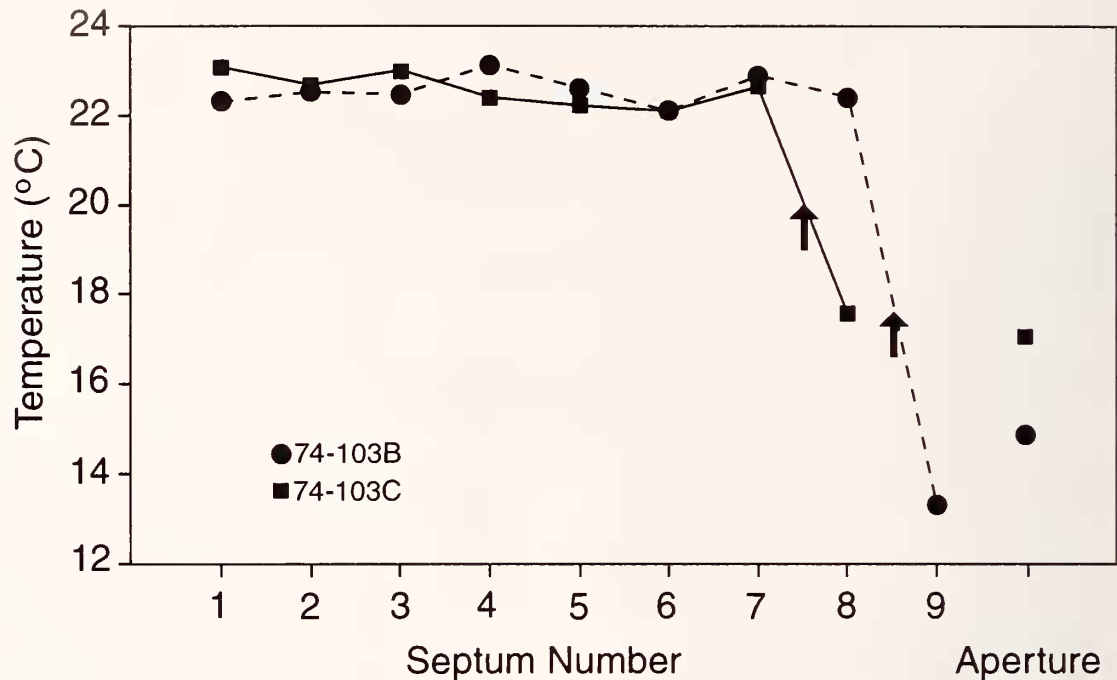


Figure 4. Calculated temperatures of the water in which the septa and apertural margin formed in specimens 74-103B and 74-103C. Septa are numbered in their order of secretion. The arrows indicate the point of hatching on each specimen.

tance between a depth of 370 m on the steep slope of the outer reef face and a depth of 1 m in the shallow lagoon near the site of capture is only 1.5 km.

One possibility is that storms transported the animals upslope. There is little meteorological information available for the time of capture of the specimens. However, Davis & Mohorter (1973) did not report any unusual weather conditions in the months prior to collection. In any event, it is unlikely that storms would have had any effects on water depths of as much as 370 m.

A second possibility is that the animals swam into shallow water. Diurnal migrations of *Nautilus* have been documented at several sites in the Pacific but not in Fiji. In Palau, *Nautilus* inhabit depths of 250–350 m during the day and migrate into shallower water (100–150 m deep) at night (Carlson et al., 1984; Ward et al., 1984). In New Caledonia, specimens have occasionally been caught at night at depths between 5 and 10 m (Ward & Martin, 1980). In Fiji, a few specimens have been caught at depths of as little as 100 m, but most have been caught in deeper water (Ward & Martin, 1980; Ward, 1987; Hayasaka et al., 1987).

The most likely explanation is that the newly hatched animals swam part way up the slope, perhaps to a depth of 100–200 m. Such small animals would not have been very powerful swimmers (Chamberlain, 1978), and upwelling currents then could have carried them the rest of the way through the passage in the reef into the shallow lagoon. Once there, the animals were probably unable to

return to their normal depth. Although they concealed themselves in a rock crevice, it was only a matter of time before a predator (or collector) caught them, or death otherwise intervened.

Drifted shells of newly hatched *Nautilus* have been reported from several localities. In Fiji, four such shells were collected off Vanua Levu (Davis & Mohorter, 1973). Two of these for which there are data range from 22 to 24 mm in diameter (Davis & Mohorter, 1973:pl. 1, fig. 7, table 1). One has seven septa without septal approximation, and the other has eight septa with septal approximation between the last two septa. Both specimens lack the nepionic constriction, indicating no growth of the outer shell after hatching. Arnold et al. (1987:398) also commented on the occurrence of such shells, one of which, from the Philippines, is illustrated in Figures 2E–G. It is probable that all of these drifted individuals hatched at depths of 100–200 m, depending on the location, and were subsequently transported, possibly by currents, up the reef slope where they became stranded and died.

Acknowledgments. We thank Dr. Nigel Hughes (formerly at the Cincinnati Museum of Natural History, now at the University of California, Riverside) and Dr. Colin Sumrall (CMNH) for their kind permission to sample the specimens in their care. We thank Dr. J. Kirk Cochran (State University of New York, Stony Brook) for helpful suggestions and reviewing an early draft of this manuscript. Ms. Susan Kiofak (American Museum of Natural History) sectioned the specimens, Mr. Irv Quitmyer (Florida Museum of Natural History) and Dr. Jason Curtis (Department of

Geology, University of Florida) helped prepare and analyze the isotopic samples, Ms. Martha Singer-Small and Ms. Bushra Hus-saini (both AMNH) located the temperature-depth profiles and bathymetric charts for Fiji. Mr. Stephen Thurston (AMNH) prepared the figures, and Ms. Stephanie Crooms (AMNH) word-processed the manuscript. Ms. Michelle Eldredge collected and donated the fine specimen of *Nautilus pompilius* from the Phil-ippines (AMNH 44681).

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